Empirical Tests of Biased Body Size Distributions in Aquatic Snake Captures

John D. Willson[1], Christopher T. Winne[1], and Michael B. Keck[2]

Ecologists often rely on a suite of demographic parameters—such as age structure, body size distributions, population density, and sex ratios—to understand life history patterns, population dynamics, and community structure of snakes. Unfortunately, in many cases little consideration is given to how sampling techniques may influence the outcome of demographic studies. Herein, we use a combination of field capture techniques, an extensive database of field-captured snakes, and laboratory and field experiments to evaluate how capture methods may influence demographic assessments of several North American semi-aquatic snake species, including *Agkistrodon piscivorus*, *Farancia abacura*, *Nerodia fasciata*, *N. floridana*, *N. rhombifer*, *N. taxispilota*, *Regina rigida*, *Seminatrix pygaea*, and *Thamnophis sauritus*. We found that commercially available aquatic funnel traps (i.e., minnow traps) generally yielded biased assessments of population demography, but that the nature and magnitude of these biases varied predictably by species and trap type. Experimental manipulations of funnel opening diameter in aquatic funnel traps demonstrated that such modifications allowed for capture of larger snakes but that the size of funnel opening necessary to capture the largest individuals varied between species. Additionally, we found differences between snake species in their ability to escape from different types of traps at birth, suggesting that escape of neonates through trap mesh can lead to the lack of small snakes often observed in field samples. Overall, our results demonstrate that capture methods may bias assessments of snake population demography, but that careful design of sampling methodology, with consideration of potential biases, can yield meaningful data on snake biology.

DEMOGRAPHY, the statistical study of populations, especially with reference to age, size, density, and distribution, provides a key to understanding life history patterns, population dynamics, and community composition, all of which have obvious applications to conservation biology. Indeed, snake population demography has been the foundation for many studies of snake ecology and conservation (Plummer, 1985; Brown and Weatherhead, 1999; Blouin-Demers et al., 2002). Moreover, because snakes exhibit cryptic behavior and low or sporadic activity patterns, demography is often used as a proxy for direct monitoring of population parameters (Madsen and Shine, 2000; Lacki et al., 2005; Willson et al., 2006). Unfortunately, knowledge of how sampling methodology influences the assessment of snake population demography is limited (but see Prior et al., 2001). For example, newborn and juvenile snakes are often under-represented in demographic studies, a phenomenon generally interpreted as evidence for high juvenile mortality (Parker and Plummer, 1987). However, sampling biases are seldom assessed with sufficient rigor to reject the alternative hypothesis that a paucity of small snakes may be due to ineffective sampling techniques for juveniles.

Adequate assessment of population demography requires standardized sampling techniques with a thorough understanding of inherent methodological biases. Nonetheless, many studies abandon systematic or randomized sampling in favor of opportunistic or haphazard methods to maximize captures and avoid the logistical difficulties associated with statistically rigorous sampling of rare or secretive snakes (Parker and Plummer, 1987; Prior et al., 2001; Willson et al., 2005). Population studies that employ standardized snake collection techniques have been conducted mostly in habitats with unusually high snake density (Godley, 1980; Sun et al., 2001; Luiselli, 2006). However, even in these situations, sampling biases seldom have been critically examined (but see Rodda, 1993; Sun et al., 2001; Rodda et al., 2005). Inherent biases exist with all techniques and sound experimental design requires knowledge of sampling biases before appropriate conclusions can be made.

The demography of semi-aquatic snakes has received considerable attention in the literature (Shine, 1986a, 1986b; Houston and Shine, 1994; King et al., 1999), and has been a major area of investigation in our own ecological research (Winne et al., 2005, 2006a; Willson et al., 2006). Commonly used techniques for sampling aquatic snakes include visual encounter surveys (Rodda, 1993; Sun et al., 2001), flipping natural or artificial cover objects (i.e., "coverboards;" Grant et al., 1992; Parmelee and Fitch, 1995; Webb and Shine, 2000), road cruising (Fitch, 1987), terrestrial pitfall or funnel trapping (often in conjunction with drift-fences; Fitch, 1951; Gibbons and Semlitsch, 1981; Enge, 1997), and aquatic funnel trapping (Keck, 1994). Among these methods, passive capture techniques (i.e., trapping) are particularly useful because they are less prone to observer biases than active survey methods (e.g., visual surveys; Rodda, 1993) and reduce biases in capture probability caused by short-term shifts in environmental conditions because captures are integrated over time (Willson and Dorcas, 2003). First described by Keck (1994), aquatic funnel trapping using commercially available "minnow," "craw-

[1] Savannah River Ecology Laboratory, University of Georgia, Drawer E, Aiken, South Carolina 29802; E-mail: (JDW) willson@uga.edu; and (CTW) ctwinne@uga.edu. Send reprint requests to JDW.
[2] Grayson County College, 6101 Grayson Drive, Denison, Texas 75020; E-mail: mikebkeck@yahoo.com.
Submitted: 7 February 2007. Accepted: 24 September 2007. Associate Editor: M. J. Lannoo.
 DOI: 10.1643/CH-07-035

Table 1. Characteristics of Cylindrical Funnel Traps Used to Capture Snakes in Aquatic Habitats.

Trap type	Length (cm)	Diameter (cm)	Funnel extension (cm)	Funnel opening diameter (cm)	Max mesh size (cm)	Price (U.S.)
Plastic minnow	43	16	11	2.5	0.4 × 0.6[a]	$7.25
Galvanized steel minnow	42	19	11	2.5[b]	0.6 × 0.6	$8.96
Galvanized steel eelpot	80	20	11[c]	2.5[b]	0.6 × 0.6	$17.25

[a] Mesh size ranges from 0.1 × 0.3–0.4 × 0.6 cm.
[b] Funnel openings of steel and eelpot traps may be widened. Funnel openings of eelpot traps used in Texas were widened to 3.8 or 5.1 cm to investigate how much they must be widened to allow for capture of the largest snakes (see Methods). Some steel minnow traps used in South Carolina were widened to ca. 3.0–3.5 cm.
[c] Funnels of eelpot traps used in this study were extended to approximately 20 cm by attaching an additional 9-cm piece of steel mesh to the widened funnel opening.

fish,'' or ''eelpot'' traps has recently emerged as an effective method for sampling semi-aquatic snake species (Seigel et al., 1995; Willson et al., 2005; Winne, 2005). Several types of aquatic traps are commercially available under various regional names; however, for the purposes of this study we refer to standard ''gee'' traps as ''minnow traps'' and ''gee'' traps with a central extension as ''eelpot traps'' (Table 1). Although previous studies have suggested that aquatic funnel trap captures may be biased towards actively foraging snakes (Keck, 1994; Winne, 2005), the potential for sampling methodology to bias demographic data has seldom been evaluated.

Herein we use a combination of laboratory experiments and an extensive database of field-captured snakes to evaluate size biases of several North American semi-aquatic snake species captured in commercially-available aquatic funnel traps. Specifically, we (1) compare body size distributions of field-captured snakes among sampling techniques to determine if aquatic traps capture all sizes of snakes present within the population, (2) manipulate the size of funnel trap openings to determine the role of funnel opening diameter in limiting the upper body size of snakes captured in traps, and (3) experimentally release neonates of seven snake species into aquatic funnel traps at birth and after a period of growth, to test the hypothesis that trap mesh width limits the lower body size distribution of snakes captured in different trap types. Our results demonstrate that capture methods may bias assessments of snake population demography, but that careful design of sampling methodology, with consideration of potential biases, can yield meaningful data on snake biology.

MATERIALS AND METHODS

Field capture methods.—With the exception of *Nerodia rhombifer* and *Agkistrodon piscivorus* (see below), we collected all snakes on the U.S. Department of Energy's Savannah River Site (SRS), located in Aiken and Barnwell Counties, South Carolina, U.S.A. We captured most snakes from aquatic habitats including Carolina bays and other temporary freshwater wetlands, natural and man-made permanent ponds, freshwater streams, creeks, and the Savannah River. A large proportion of captures were from Ellenton Bay, a 10-ha semi-permanent Carolina bay freshwater wetland and the site of several long-term snake population studies (Seigel et al., 1995; Winne et al., 2005, 2006a; Willson et al., 2006; Glaudas et al., 2007).

Snakes were captured using aquatic funnel traps and ''other methods.'' We used two aquatic funnel trap types (Table 1), frequently marketed to capture live minnows and crayfish for fishing bait, for trap comparisons of body size distributions on the SRS: galvanized steel (''1/4-inch hardware cloth'') cylindrical minnow traps (model G-40; Cuba Specialty Manufacturing Company, Fillmore, NY) and plastic cylindrical minnow traps (model 700; N.A.S. Incorporated, Marblehead, OH). We used plastic traps as purchased from the manufacturer, but we widened funnel openings (i.e., the entrances into the trap) to ca. 3–3.5 cm in some steel traps by forcing a wooden dowel through the funnel opening. We set funnel traps in shallow water with approximately 3–5 cm of the trap remaining above water level and checked traps daily for snakes. We did not intentionally bait traps, although incidental captures of fish and amphibians often resulted in ''natural baiting'' (Keck, 1994; Winne, 2005). ''Other'' capture methods included searching for snakes under aquatic and terrestrial artificial coverboards (including wood and metal; Grant et al., 1992), terrestrial drift fences with pitfall or funnel traps (Fitch, 1951; Gibbons and Semlitsch, 1981), road collecting (Fitch, 1987), and incidental hand captures. For comparisons with aquatic trap captures, we combined captures made with all ''other methods'' to generate unbiased assessments of the range of snake sizes available for capture. However, because *Seminatrix pygaea* at our study site were only captured reliably using aquatic traps and coverboards, most *S. pygaea* captured using ''other methods'' were coverboard captures.

We returned all captured snakes to the laboratory, where species, sex (determined by visual inspection, probing, or manual eversion of hemipenes), SVL, and mass were recorded. All snakes with palpable food items were manually forced to regurgitate (Fitch, 1987) in order to obtain an accurate mass. Each snake was then individually marked by ventral branding (Winne et al., 2006b) or by implanting a passive integrated transponder (PIT tag) before being returned to its capture location.

Manipulation of funnel opening diameter.—To assess how much funnel openings need to be widened to allow for capture of large snakes (*N. rhombifer* and *A. piscivorus*), we trapped snakes irregularly over a 39-month period in Lake Fairfield, an artificial impoundment in Freestone County, Texas. We used galvanized steel cylindrical eelpot traps (model G-40EP; Cuba Specialty Manufacturing Company, Fillmore, NY; Table 1) with funnel openings widened to either 3.8 or 5.1 cm by cutting the steel mesh. The funnels were

Table 2. **Retention of Neonate Aquatic Snakes in Plastic and Steel Minnow Traps over a One-Hour Period.** Trap entrances were blocked; thus, escapes represent snakes that passed through the trap mesh. Lab-born snakes were tested after their first shed but before ingesting their first meal. Field-captured (FC) snakes were tested soon after birth (see Methods for details). Mass for one *T. sauritus* was not recorded (NR).

Species	*n* (# litters)	Mean SVL (mm) ± SE	Mean mass (g) ± SE	Plastic trap % retained	Steel trap % retained
Nerodia taxispilota	24 (4)	233.2 ± 1.41	10.6 ± 0.17	100	100
Nerodia floridana	2 (1)	180.5 ± 0.50	7.1 ± 0.18	100	100
Nerodia fasciata	24 (4)	164.6 ± 1.75	4.2 ± 0.05	100	0
Farancia abacura	1 (FC)	192.0	5.3	100	0
Seminatrix pygaea	24 (10)	108.7 ± 0.76	1.2 ± 0.03	0	0
Regina rigida	5 (1)	137.2 ± 3.79	3.1 ± 0.29	0	0
Thamnophis sauritus	2 (FC)	153, 151	1.18, NR	0	0

extended to approximately 20 cm by attaching an additional 9-cm piece of steel mesh to the widened funnel opening (Keck, 1994). The traps were baited with dead fish, primarily *Lepomis* sp., and placed half-submerged along the shoreline, with the funnel openings just below the surface of the water.

Experimental neonate escape trials.—During aquatic funnel trapping, we observed differences in capture rates between adult and neonate snakes and that the magnitude of these differences varied among species differing in neonate body size. Consequently, we designed an experiment to test the propensity of neonates of different species to escape through the mesh of traps. To obtain experimental subjects, we captured pregnant female snakes (*N. fasciata* [*n* = 4], *N. floridana* [*n* = 1], *N. taxispilota* [*n* = 4], *Regina rigida* [*n* = 1], and *S. pygaea* [*n* = 10]) by hand or in aquatic funnel traps on the SRS and maintained them in the laboratory until parturition (see Hopkins et al., 2005 and Hopkins and Winne, 2006 for general housing details). After parturition, we selected lab-born neonates haphazardly from each litter (*N. fasciata* [*n* = 24], *N. floridana* [*n* = 2], *N. taxispilota* [*n* = 24], *R. rigida* [*n* = 5], and *S. pygaea* [*n* = 24]; Table 2) and tested their initial propensity to escape from traps within 30 days of birth, after undergoing their first shed but prior to their first feeding. In addition, we tested one hatchling *Farancia abacura* (captured prior to first shed) and two neonate *Thamnophis sauritus* captured by hand on the SRS.

Subsequent to initial tests we maintained the 24 neonate *N. fasciata* in the laboratory to examine growth-related changes in escape propensity. We housed neonate *N. fasciata* in 37.85 L aquaria with large water bowls, basking lamps (12L:12D, approx. 23–38°C gradient), plastic hide-boxes, and paper towel substrate and offered them food (*Gambusia holbrooki* or *Ambystoma talpoideum* larvae) *ad libitum* once per week. We re-tested *N. fasciata* approximately once per month until they could no longer escape through trap mesh. Prior to each trial, we measured mass, SVL, and head width at the widest point of the head (nearest mm using a squeeze box; Quinn and Jones, 1974). All snakes were post-absorptive during trials.

We tested all neonates for propensity to escape through mesh of both steel and plastic traps on separate but consecutive days between 0800 and 1600 h. Prior to escape trials, we sealed trap funnel openings and slightly bent adjoining hinges around the central seam of steel traps to create a snug seal. Together, these methods ensured that the only possible escape route for neonates was through the trap mesh. We conducted escape trials inside 37.85 L aquaria with steel mesh lids, set within an environmental chamber at 30°C. We set one trap in each aquarium, filled with water (30°C) to a depth of 12 cm to mimic field trapping conditions. We placed four paper towels in the water around each trap to provide structural support for escaped snakes. We released neonate snakes into traps (<5 per trap) and subsequently censused traps every 15 min for 1 h. At each observation we removed all escaped neonates to prevent them from re-entering traps before the termination of the trial.

Data analyses.—To evaluate capture biases of aquatic funnel traps, we examined body size distributions of snakes captured in the field using different trap types. Because we were interested in understanding any potential biases associated with various methods of field data collection, we did not rely on statistical comparisons, but rather relied on a more conservative approach—visual inspection of data plots. We included all recaptured snakes in our comparisons because each capture represents a unique size of snake that was able to enter a trap. Therefore, some data points in the figures represent multiple captures of the same individual.

RESULTS

Field captures.—Body size distributions of *S. pygaea* captured on the SRS (*n* = 1214) differed substantially among capture methods (Fig. 1). *Seminatrix pygaea* size at birth was 109.9 ± 0.88 mm SVL (grand mean ± SE; *n* = 42 litters) on the SRS. Coverboards captured snakes of nearly all sizes, ranging from those just larger than size at birth to large adults (Fig. 1A). Plastic traps did not capture the smallest *S. pygaea*. With the exception of one outlier (SVL: 127 mm), which likely could have escaped from the trap, *S. pygaea* did not become catchable in plastic traps until they reached ca. 180 mm SVL (Fig. 1B). A small size range of *S. pygaea* (180–280 mm SVL) was vulnerable to entanglement in the mesh of plastic traps (Fig. 1C). Steel traps only captured *S. pygaea* greater than 250 mm SVL and were capable of entangling individuals up to at least 325 mm SVL (Fig. 1D). The lack of large *S. pygaea* in our relatively small sample captured in steel traps was not due to trap bias. Rather, this was due to our limited sampling of *S. pygaea* with steel traps, during a brief period when large individuals were scarce (2003; CTW and JDW, unpubl. data). We subsequently chose to discontinue use of steel traps for *S. pygaea* to avoid mortality of larger (sometimes pregnant), entangled snakes. Nonethe-

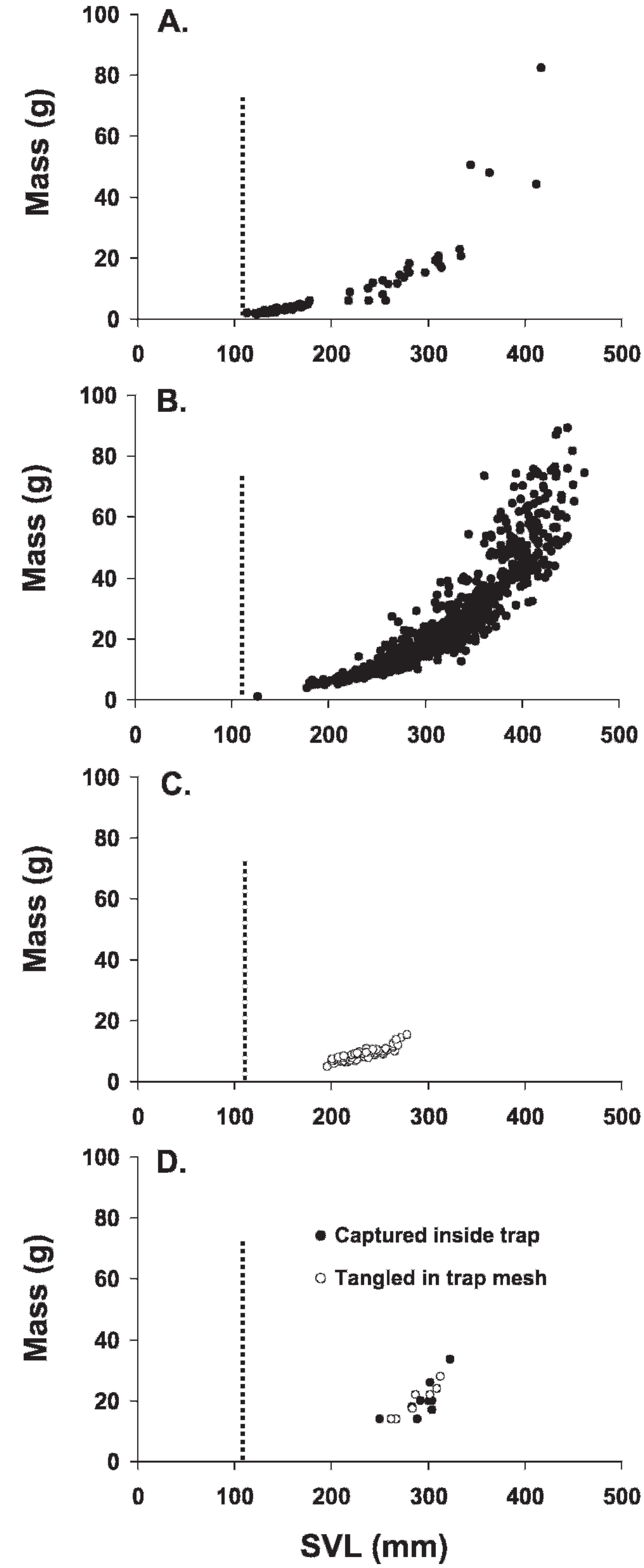

Fig. 1. Length–mass relationships of *S. pygaea* (n = 1214) captured using different methods on the Savannah River Site in South Carolina—(A) snakes captured using methods other than aquatic funnel traps (primarily coverboard captures), (B) snakes captured inside plastic minnow traps but not tangled in mesh, (C) captured snakes tangled in the mesh of plastic traps, (D) snakes captured inside or tangled in mesh of steel minnow traps. Vertical dashed lines represent mean size at birth based on 462 neonates from 42 litters. Open circles in (C) and (D) represent snakes that were tangled in the mesh of traps, many of which were dead upon capture. The lack of large *S. pygaea* in steel trap captures (D) is not due to trap bias, but rather to a combination of small sample size and lack of large individuals during the time period when steel traps were used (see Results).

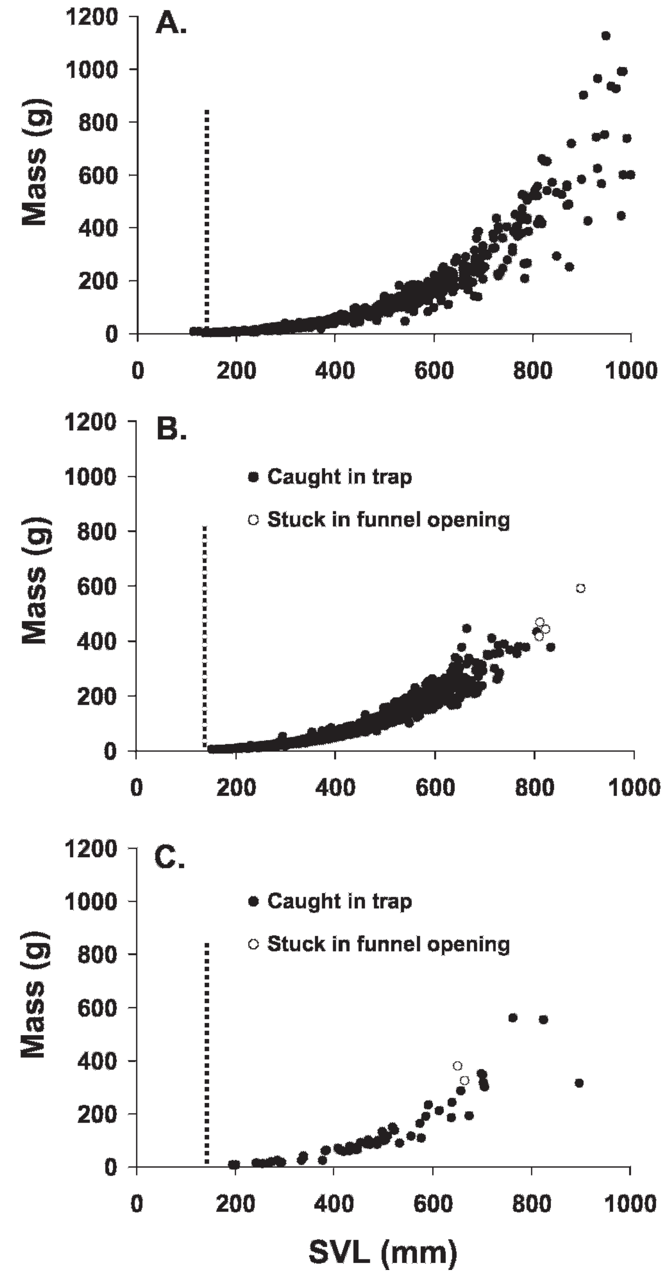

Fig. 2. Length–mass relationships of *N. fasciata* (n = 1930) captured using different methods on the Savannah River Site in South Carolina—(A) methods other than aquatic funnel traps, (B) plastic minnow traps, (C) steel minnow traps. Vertical dashed lines represent mean size at birth based on 65 neonates from eight litters. Funnel openings of some steel traps were widened to ca. 3–3.5 cm. Open circles in (B) and (C) represent snakes that were stuck (wedged) in the funnel opening and thus were captured but were unable to fully enter the trap.

less, we do not doubt that steel traps were capable of capturing even the largest *S. pygaea*.

Body size distributions of *N. fasciata* captured on the SRS (n = 1930) also differed substantially among capture methods (Fig. 2). At birth, *N. fasciata* from the SRS averaged 150.59 ± 3.40 mm SVL (grand mean ± SE; n = 8 litters). The largest adults were ca. 1000 mm SVL and up to 1125 g in mass, and were captured using "other methods" (Fig. 2A). *Nerodia fasciata* captured in plastic traps ranged from those just larger than size at birth to ca. 830 mm SVL; however, at larger SVLs only relatively slim individuals (i.e., those with low mass relative to SVL) were captured (Fig. 2B). A few

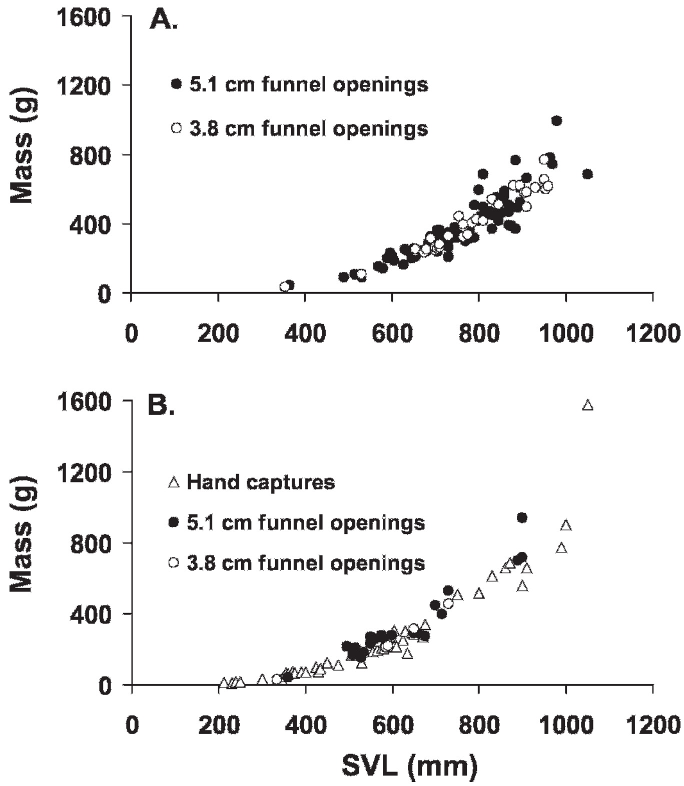

Fig. 3. Length–mass relationships of (A) *N. rhombifer* (n = 128) and (B) *A. piscivorus* (n = 86) captured in Texas using steel eelpot traps with funnel openings widened to 3.8 or 5.1 cm. Note that for *N. rhombifer*, snakes of similar size were caught in both trap types. For *A. piscivorus*, snakes caught by hand and in traps with 5.1 cm funnel openings were of similar size, but snakes caught in traps with 3.8 cm funnel openings were substantially smaller.

larger individuals were occasionally captured in plastic traps after becoming stuck (wedged) in the funnel opening, but such entanglement did not result in mortality. Steel traps, especially those with widened funnel openings, were capable of capturing larger *N. fasciata* (to ca. 900 mm SVL), but only captured juveniles ca. 200 mm SVL or larger (Fig. 2C). Additionally, two relatively heavy-bodied snakes became stuck in funnel openings of steel traps (both had unwidened, 2.5 cm funnel openings), resulting in mortality on both occasions.

Funnel opening diameter.—Steel eelpot traps with funnel openings widened to 3.8 or 5.1 cm effectively captured *N. rhombifer* and *Agkistrodon piscivorus* at a site in eastern Texas. Although the largest *N. rhombifer* (980 mm SVL, 992 g) was captured in a trap with a 5.1 cm funnel opening, both opening sizes were capable of capturing *N. rhombifer* up to their maximum size at that locality (Fig. 3A). Relatively few *A. piscivorus* were captured in traps with 3.8 cm funnel openings and the largest *A. piscivorus* captured in a trap with 3.8 cm openings (SVL: 730 mm, mass: 455 g) was substantially smaller than the largest captured in a trap with 5.1 cm openings (SVL: 900 mm, mass: 940 g; Fig. 3B). Additionally, with the exception of one extremely large outlier, the range of sizes of *A. piscivorus* captured in traps with 5.1 cm openings was similar to that of *A. piscivorus* captured by hand at that site (Fig. 3B).

Neonate escape trials.—Of the seven species of semi-aquatic snakes tested, only *N. taxispilota* and *N. floridana* were unable to escape through the mesh of steel traps at birth (Table 2). All newborn *N. fasciata*, and the one neonate *F. abacura* we tested, escaped through the mesh of steel traps but were unable to escape from plastic traps. Newborn *S. pygaea*, *R. rigida*, and *T. sauritus* could all escape through the mesh of both trap types.

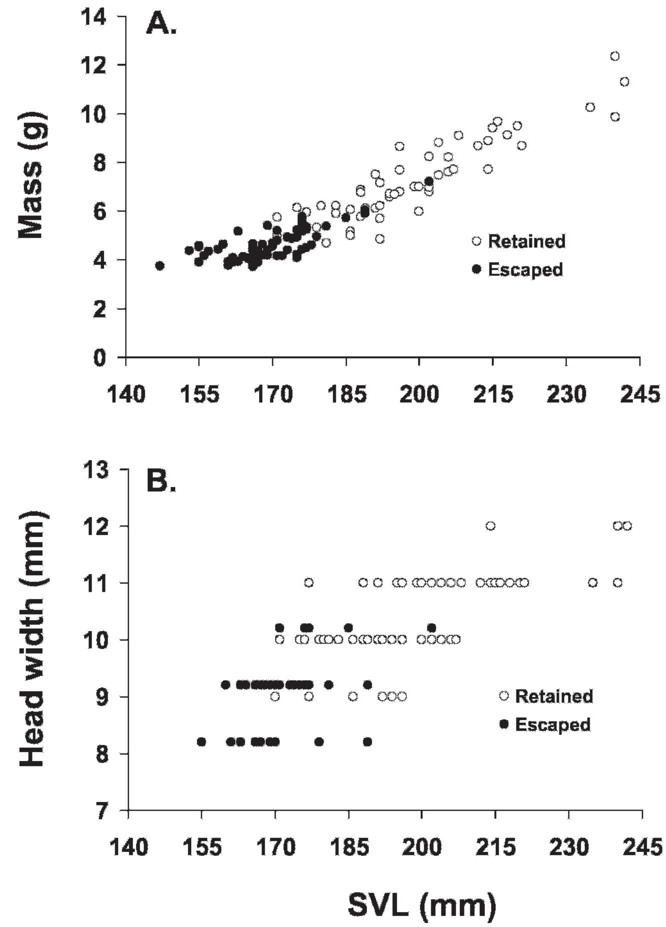

Fig. 4. Ontogenetic shifts in retention of neonate *N. fasciata* in steel minnow traps due to growth. (A) Retention as a function of length (SVL) and mass for 24 *N. fasciata* tested repeatedly over a three-month period of growth. (B) Retention as a function of head width for the same snakes. Retained snake head widths (•) in (B) are offset slightly to ease examination.

At birth, all *N. fasciata* could escape through the mesh of steel traps (Table 2). As they grew, fewer *N. fasciata* could escape and nearly all were retained at sizes greater than 190 mm SVL (Fig. 4A). Correspondingly, no *N. fasciata* with head widths less than 9 mm were retained in traps (Fig. 4B). At 10-mm head width, most *N. fasciata* were retained, and at 11-mm head width all were retained.

DISCUSSION

We used a combination of field data on snakes collected using various methods and experimental releases of neonate snakes into traps in the laboratory to test for biases in demography of snakes captured using aquatic funnel traps. We found that traps generally yielded biased assessments of population demography, but that the nature and magnitude of these biases varied predictably by species and trap type. Experimental manipulations of funnel opening diameter in steel traps demonstrated that such modifications allowed for capture of larger snakes but that the size of funnel opening necessary to capture the largest individuals varied between species. Finally, we found differences between snake species in their ability to escape from different types of traps at birth, suggesting that escape of neonates through trap mesh can cause the lack of small snakes often observed in field samples. Our results highlight the importance of considering potential sampling biases when selecting a sampling technique and designing a sampling scheme.

Sampling for juveniles and small species.—In studies of population dynamics or for conservation-oriented population assessments, detection of hatchling and juvenile snakes is often a priority. In many cases, juvenile snakes are underrepresented in demographic samples and this paucity of small individuals is often attributed to low juvenile survivorship (Parker and Plummer, 1987). We demonstrate that differences exist between aquatic funnel trap types in their ability to capture small snakes and thus lack of juveniles in samples may reflect a bias of the sampling method rather than real differences in relative abundance among age classes. We found that only aquatic snakes with large young (e.g., *N. floridana*, *N. taxispilota*, and likely *N. rhombifer*) were catchable in steel traps from birth and that juveniles of large species with smaller young may not become catchable in steel traps until they have grown considerably. For example, the smallest *N. fasciata* captured in steel traps were ca. 40 mm SVL larger than mean size at birth. Moreover, in *Nerodia* the ability to escape appears to be largely a function of head width, with neonate *N. fasciata* losing the ability to escape from steel traps once their head width reaches ca. 10–11 mm. However, for species with smaller relative head sizes (e.g., *S. pygaea*, *F. abacura*) the ability to escape may be limited by maximum body diameter. Indeed, small *S. pygaea* often became entangled at mid-body in trap mesh, sometimes resulting in mortality. Plastic traps have the smallest trap mesh and smallest funnel openings of any of the traps we examined (Table 1) and were generally much more effective than steel traps for capturing small individuals and species. When sampling small species (e.g., *S. pygaea*), entanglement and mortality of captured snakes is a major concern. We found that plastic traps entangle a much smaller size range of snakes than steel traps, and we found that plastic traps do not entangle reproductively active (pregnant) females. Moreover, plastic traps contain mesh of various sizes and entangled snakes nearly always entangle themselves in the single largest row of mesh (located around the central seam of the trap; JDW and CTW, pers. obs.). It is likely that modifying plastic traps to seal this row of mesh would virtually eliminate snake entanglement in plastic traps. Thus, we recommend plastic traps for sampling small species and for sampling large species with small young (e.g., *N. fasciata*, *N. sipedon*) when juvenile snakes are a target group. However, it is important to remember that newborns of small species (e.g., *S. pygaea*, *R. rigida*, *T. sauritus*) can escape through mesh of plastic traps. For example, *S. pygaea* could escape from plastic traps at birth and apparently did not become catchable until they reached ca. 180 mm SVL. It is possible that using traps without mesh would be effective for sampling species with very small young. Such traps have been used to capture small terrestrial snakes (Clark, 1966) as well as amphibians within aquatic habitats (Willson and Dorcas, 2003).

Sampling for large species or life stages.—A first step in designing a sampling scheme that provides an unbiased assessment of population size structure is determining that all sizes or species of interest can be captured. We found that large individuals of the larger semi-aquatic snake species (e.g., *Nerodia* sp. and *A. piscivorus*) are not catchable with all trap types. For example, *N. fasciata* are not captured in plastic traps once they reach ca. 830 mm SVL, but smaller snakes may be excluded if they are heavy for their length (e.g., pregnant females). Undoubtedly, as purchased from the manufacturer, steel traps also exclude large snakes but these traps may be modified to widen funnel openings. We found that widening the funnel opening permits capture of large snakes, but that the diameter to which openings must be widened varies by species and is likely a function of head width. In *N. rhombifer*, widening the funnel openings to 3.8 cm allowed capture of even the largest individuals. Alternatively, for *A. piscivorus*, which have relatively larger heads, 5.1 cm funnel openings were necessary to trap large individuals. An additional consideration is that in sexually dimorphic species, exclusion of the largest individuals can lead to biased assessments of population sex ratio, or biased assessments of reproductive parameters if the largest females are not sampled. Consequently, we recommend using steel minnow or eelpot traps with widened funnel openings when targeting adults of such large species. However, if funnel openings are enlarged too much, significant numbers of snakes may escape, particularly if funnel extensions (Keck, 1994) are not used. Keck (1994) found that eelpot traps with funnel openings enlarged to 6.3 cm caught fewer snakes than traps with 4 or 5 cm openings, but traps with 4 and 5 cm openings caught similar numbers. Additionally, we caution that large snakes occasionally become stuck in the funnel opening of both plastic and steel traps. Under such circumstances, the sharp edges of steel funnel openings can injure or even kill snakes. Therefore, when enlarging funnel openings, we use pliers to fold the sharp steel edges away from the opening.

In most cases population studies and monitoring initiatives require representative sampling of all individuals within the population. Our data provide a guide to determine what types of aquatic funnel traps must be used to ensure that all species or size classes of interest are potentially sampled. In many cases, using a combination of several trap types may be the best strategy to capture all age classes within a population or sample an aquatic snake community with several species that vary in size. Although traps may be capable of sampling all sizes of snakes, composition of trap captures should not necessarily be interpreted as unbiased samples of the population. Trap capture rates are indices of relative abundance that are influenced by multiple factors, including snake density, activity patterns, habitat preferences, and propensity of individuals to escape from traps (Willson et al., 2005), among others. Thus, ideally comparisons of capture rates should be combined with mark–recapture analyses or other methods for estimating population parameters. We encourage further laboratory and field tests of sampling bias designed to increase the ability of researchers and land managers to accurately interpret snake demographic data (Prior et al., 2001; Sun et al., 2001; Rodda et al., 2005), especially for species where recapture rates are low and relative abundance is often the most feasible measure for population monitoring.

ACKNOWLEDGMENTS

We thank all members of the Savannah River Ecology Laboratory who helped capture or process snakes used in this study, especially K. Andrews, A. Durso, E. Eskew, L. Fedewa, J. Gibbons, X. Glaudas, J. Greene, T. Luhring, R. Seigel, T. Tuberville, and C. Young. A. Durso and J. Gibbons provided insightful comments on earlier versions of this manuscript. All procedures used in the study were approved by the University of Georgia animal care and use committee #A2003-10024, #A2005-10102-m1, and #A2006-10229-0. This material is based upon work supported by the Department of Energy under Award Number DE-FC09-07SR22506 to the University of Georgia Research Foundation.

LITERATURE CITED

Blouin-Demers, G., K. A. Prior, and P. J. Weatherhead. 2002. Comparative demography of black rat snakes (*Elaphe obsoleta*) in Ontario and Maryland. Journal of Zoology, London 256:1–10.

Brown, G. P., and P. J. Weatherhead. 1999. Demography and sexual size dimorphism in northern water snakes, *Nerodia sipedon*. Canadian Journal of Zoology 77: 1358–1366.

Clark, D. R., Jr. 1966. A funnel trap for small snakes. Transactions of the Kansas Academy of Sciences 69: 91–95.

Enge, K. M. 1997. A standardized protocol for drift-fence surveys. Florida Game and Fresh Water Fish Commission Technical Report No. 14. Tallahassee, Florida.

Fitch, H. S. 1951. A simplified type of funnel trap for reptiles. Herpetologica 7:77–80.

Fitch, H. S. 1987. Collecting and life-history techniques, p. 143–164. *In*: Snakes: Ecology and Evolutionary Biology. R. A. Seigel, J. T. Collins, and S. S. Novak (eds.). McGraw-Hill, Inc., New York.

Gibbons, J. W., and R. D. Semlitsch. 1981. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimleyana 7:1–16.

Glaudas, X., K. M. Andrews, J. D. Willson, and J. W. Gibbons. 2007. Migration patterns in a population of cottonmouths (*Agkistrodon piscivorus*) inhabiting an isolated wetland. Journal of Zoology, London 271: 119–124.

Godley, J. S. 1980. Foraging ecology of the striped swamp snake, *Regina alleni*, in southern Florida. Ecological Monographs 50:411–436.

Grant, B. W., A. D. Tucker, J. E. Lovich, A. T. Mills, P. M. Dixon, and J. W. Gibbons. 1992. The use of coverboards in estimating patterns of reptile and amphibian abundance, p. 379–403. *In*: Wildlife 2001: Populations. R. D. R. McCullough and R. H. Barrett (eds.). Elsevier Science Publishers, Inc., London.

Hopkins, W. A., and C. T. Winne. 2006. Influence of body size on swimming performance of four species of neonatal natricine snakes acutely exposed to a cholinesterase-inhibiting pesticide. Environmental Toxicology and Chemistry 25:1208–1213.

Hopkins, W. A., C. T. Winne, and S. E. DuRant. 2005. Differential swimming performance of two Natricine snakes exposed to a cholinesterase-inhibiting pesticide. Environmental Pollution 133:531–540.

Houston, D., and R. Shine. 1994. Population demography of Arafura filesnakes (Serpentes, Acrochordidae) in tropical Australia. Journal of Herpetology 28:273–280.

Keck, M. B. 1994. A new technique for sampling semi-aquatic snake populations. Herpetological Natural History 2:101–103.

King, R. B., T. D. Bittner, A. Queral-Regil, and J. H. Cline. 1999. Sexual dimorphism in neonate and adult snakes. Journal of Zoology, London 247:19–28.

Lacki, M. J., J. W. Hummer, and J. L. Fitzgerald. 2005. Population patterns of copperbelly water snakes (*Nerodia erythrogaster neglecta*) in a riparian corridor impacted by mining and reclamation. American Midland Naturalist 153:357–369.

Luiselli, L. 2006. Interspecific relationships between two species of sympatric Afrotropical water snake in relation to a seasonally fluctuating food resource. Journal of Tropical Ecology 22:91–100.

Madsen, T., and R. Shine. 2000. Rain, fish and snakes: climatically driven population dynamics of Arafura filesnakes in tropical Australia. Oecologia 124: 208–215.

Parker, W. S., and M. V. Plummer. 1987. Population ecology, p. 253–301. *In*: Snakes: Ecology and Evolutionary Biology. R. A. Seigel, J. T. Collins, and S. S. Novak (eds.). McGraw-Hill, Inc., New York.

Parmelee, J. R., and H. S. Fitch. 1995. An experiment with artificial shelters for snakes: effects of material, age, and surface preparation. Herpetological Natural History 3:187–191.

Plummer, M. V. 1985. Demography of green snakes (*Opheodrys aestivus*). Herpetologica 41:373–381.

Prior, K. A., G. Blouin-Demers, and P. J. Weatherhead. 2001. Sampling biases in demographic analyses of black rat snakes (*Elaphe obsoleta*). Herpetologica 57: 460–469.

Quinn, H., and J. P. Jones. 1974. Squeeze box technique for measuring snakes. Herpetological Review 5:35.

Rodda, G. H. 1993. Where's Waldo (and the snakes)? Herpetological Review 24:44–45.

Rodda, G. H., K. Dean-Bradley, and T. H. Fritts. 2005. The predictive power of visual searching. Herpetological Review 36:259–264.

Seigel, R. A., J. W. Gibbons, and T. K. Lynch. 1995. Temporal changes in reptile populations: effects of a severe drought on aquatic snakes. Herpetologica 51:424–434.

Shine, R. 1986a. Ecology of a low-energy specialist: food habits and reproductive biology of the arafura filesnake (Acrochordidae). Copeia 1986:424–437.

Shine, R. 1986b. Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. Oecologia 69:260–267.

Sun, L., R. Shine, Z. Debi, and T. Zhengren. 2001. Biotic and abiotic influences on activity patterns of insular pit-vipers (*Gloydius shedaoensis*, Viperidae) from north-eastern China. Biological Conservation 97:387–389.

Webb, J. K., and R. Shine. 2000. Paving the way for habitat restoration: Can artificial rocks restore degraded habitats of endangered reptiles? Biological Conservation 92:93–99.

Willson, J. D., and M. E. Dorcas. 2003. Quantitative sampling of stream salamanders: a comparison of dipnetting and funnel trapping techniques. Herpetological Review 34:138–140.

Willson, J. D., C. T. Winne, M. E. Dorcas, and J. W. Gibbons. 2006. Post-drought responses of semi-aquatic snakes inhabiting an isolated wetland: insights on different strategies for persistence in a dynamic habitat. Wetlands 26:1071–1078.

Willson, J. D., C. T. Winne, and L. A. Fedewa. 2005. Unveiling escape and capture rates of aquatic snakes and salamanders (*Siren* spp. and *Amphiuma means*) in commercial funnel traps. Journal of Freshwater Ecology 20:397–403.

Winne, C. T. 2005. Increases in capture rates of an aquatic snake (*Seminatrix pygaea*) using naturally baited minnow traps: evidence for aquatic funnel trapping as a measure of foraging activity. Herpetological Review 36:411–413.

Winne, C. T., M. E. Dorcas, and S. M. Poppy. 2005. Population structure, body size, and activity patterns of the black swamp snake (*Seminatrix pygaea*) in South Carolina. Southeastern Naturalist 4:1–14.

Winne, C. T., J. D. Willson, K. M. Andrews, and R. N. Reed. 2006b. Efficacy of marking snakes with disposable medical cautery units. Herpetological Review 37:52–54.

Winne, C. T., J. D. Willson, and J. W. Gibbons. 2006a. Income breeding allows an aquatic snake (*Seminatrix pygaea*) to reproduce normally following prolonged drought-induced aestivation. Journal of Animal Ecology 75:1352–1360.